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Mind over memory: Cueing the aging brain

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Abstract

A decline in recollection is a hallmark of even healthy aging and is associated with wider impairments in mental control. Older adults have difficulty internally directing thought and action in line with their goals, and often rely more on external cues. To assess the impact this has on memory, emerging brain imaging and behavioral approaches investigate the operation and effectiveness of goal directed control before information is retrieved. Current data point to effects of aging at more than one stage in this process, particularly in the face of competing goals. These effects may reflect wider changes in the proactive, self-initiated regulation of thought and action. Understanding them is essential for establishing whether internal “self-cueing” of memory can be improved, and whether - and when - it is best to use “environmental support” to maximize memory performance.

Keywords

Episodic memory, aging, cognitive control, environmental support, memory cues

Older people may experience vivid recall of events, but the devil is in the detail: did I take my medication yesterday or just think about taking it? Memory for personally experienced events (episodic memory) declines with aging, but not all aspects of memory are affected, and not only memory is affected. Can we explain that varied pattern in terms of underlying changes in a few fundamental functions, and the neural systems they depend on? An important insight has been that memory impairment is greatest on tasks requiring a high degree of deliberate control (Light, 1991). Older adults also have wider difficulties with cognitive control functions needed to flexibly regulate thoughts and actions to reflect current goals. These functions depend on the brain's prefrontal cortex, whose integrity is particularly affected by the normal aging process (see (Braver & West, 2008) for review).

Emerging research programs now seek to understand precisely how these control difficulties impede episodic memory retrieval. At any age, recollection can be easily triggered by reminders such as a song or a photo. But at other times it is very effortful. Memory is also prone to error and distortion and requires evaluation in light of our goals. To understand age effects on retrieval we must also understand effects on encoding (Rugg & Morcom, 2005). But retrieval is critical for voluntary control, and possible remediation: it is the point at which subjective difficulties often occur. Recent memory research converges with studies of control outside the memory domain to suggest that a key component of memory decline with age lies in proactive processes operating before information is retrieved. This perspective offers new insights about aging, and how we control our own ability to remember without always relying on environmental cues and prompts.

Aging, recollection and environmental support

An important clue to aging effects on episodic memory comes from findings that they are greatest when no specific cues are given (free recall), reduced when recall is cued, and often absent when the task is simply to recognize whether something has been previously encountered (Craik & McDowd, 1987). This has been explained as a failure of detailed recollection, as opposed to nonspecific recognition that something is familiar. Consistent with this, older adults are less likely to recall the jointly occurring features which make up events (associations), and context, such as when and where they took place (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). In contrast, familiarity is largely intact (Koen & Yonelinas, 2014). These difficulties may in part reflect basic problems in “binding” a unique memory trace, due to neural damage in the hippocampus. However, failures of memory control resulting from prefrontal impairment are critical (Shing et al., 2010). This prompts the question of *how* control difficulties impact recollection. Converging evidence suggests that what happens prior to the point of retrieval is critical (Morcom & Rugg, 2004).

Craik (1983) proposed that older adults have difficulty initiating the necessary processes for recall, but that given adequate environmental support from external cues, their memory difficulties can be reduced or even abolished. The self-initiation impairment is attributed to a reduction in attentional resources. In line with this, reductions in recollection of detail and associations have been reproduced in young adults given a demanding secondary task to perform during a memory test. Other studies have manipulated environmental support. Stronger

cues - for example providing four rather than three letters of words to be recalled - can boost memory more in older adults (e.g. Angel et al., 2010), although not always (Park & Shaw, 1992). Encoding words with pictures, which supports distinctive processing, helps older adults more, as can external cues (Craig & Schloerscheidt, 2011). There is evidence too that when people try not to recall, external cues remain more potent reminders for older adults (Anderson, Reinholz, Kuhl, & Mayr, 2011). Nonetheless, while some environmental support interventions do benefit older adults more, others are actually more helpful to the young, for example instructions aimed at enhancing memory strategies. This variability may reflect the degree to which acting on the provided support itself depends on self-initiated processing (for review see Luo & Craik, 2008).

Two relatively recent developments provide more traction on this important theoretical account. First, studies of attentional control have specified particular functions affected by aging. Braver's "dual mechanisms of control" theory distinguishes proactive, anticipatory control from reactive control. Under proactive control, current goals are actively maintained by prefrontal cortex, allowing these goals - rather than external events - to drive behavior. This supports self-initiated behavior and minimizes interference from competing goals. In contrast, reactive control is transient and stimulus-driven, and can only help to resolve interference once present, potentially increasing overall control demands. An example of how this may apply to episodic memory is illustrated in Figure 1, explained further below. Older adults are impaired at proactive control in attentional tasks such as the AX-CPT continuous performance task, appearing to rely on reactive control (Bugg, 2014). When some information must be maintained in temporary memory

(e.g. houses) and other information ignored (e.g. scenes), they are also less effective at selectively activating the goal-relevant information (Gazzaley, 2013).

< Insert Figure 1 about here >

The second development involves brain imaging and behavioral methods designed to study pre-retrieval control (for review see Mecklinger, 2010). Leading theories of memory control specify a role for proactive processes (Burgess & Shallice, 1996; Johnson & Raye, 2000). Effective memory cues reinstate contextual information which was incorporated in the memory trace, and trigger retrieval when they match the memory trace (Tulving, 1983). They may remind us of where something took place, or our thoughts at the time. But cues need not be external. People can strategically “self-cue” memory, by internally generating cue information or elaborating on external cues in line with their goals. For example, visualizing a particular place before seeing a photo of a person may help us recall that we previously met them in that context (Figure 1). This is one way in which people adopt a “retrieval orientation” reflecting specific retrieval goals. We may also engage a general “retrieval mode”, i.e. an attentional set conducive to retrieval. Both are also referred to in terms of control operating “at the front-end” to constrain what is retrieved (Jacoby et al., 2005). However, these processes leading to recovery of a memory are difficult to study, since they cannot be separated from retrieval itself using measures of an ultimate memory judgment (Rugg & Wilding, 2000). This may be why the behavioral studies of self-initiation and environmental support discussed earlier have had mixed findings. Brain imaging has therefore become central to understanding how pre-retrieval control works. Event-related potentials (ERPs) reflecting scalp-recorded electrical activity and

functional magnetic resonance imaging (fMRI) permit measures of how brain activity differs according to distinct retrieval goals, at different stages of retrieval. Using these approaches and novel behavioral measures we, and others, have investigated the proposal that older adults do not fully engage control processes prior to retrieval (Morcom & Rugg, 2004).

Aging and proactive control of memory

Four main experimental paradigms are used, illustrated in Figure 2. All involve an encoding (study) phase followed by a retrieval (test) phase. Items are studied in one of two alternative contexts (deep and shallow study tasks in the example in Figure 2A). This allows definition of different retrieval goals in the test phase in different blocks (or runs) of trials preceded by instructional cues. For example, participants are first asked to target the “deep” task, then the “shallow” task recognizing old items studied in the specified task (Figure 2B).

The first paradigm uses brain imaging to examine processes elicited by the instructional cues, before specific retrieval cues are even presented (Figure 2B, comparison 1). ERP studies in young adults show that preparatory neural activity depends on the type of information people have been asked to target in memory, indicating adoption of a retrieval orientation. This activity is goal-specific, distinct from preparatory activity which is common to different episodic retrieval tasks, suggesting engagement of a generic retrieval mode (Herron & Wilding, 2006).

These ERP effects have not yet been studied in aging, but a recent fMRI study showed reduced preparatory activity in hippocampus during episodic retrieval in older adults and altered connectivity with prefrontal cortex. This was consistent with impaired proactive control - either retrieval orientation or mode - although

age effects may not have been memory-specific (Dew, Buchler, Dobbins, & Cabeza, 2012). Given the substantial evidence that goal-directed preparatory attention is impaired in older adults in working memory and attention tasks (Gazzaley, 2013), this is likely to be a fruitful direction for future research.

< Insert Figure 2 about here >

The second paradigm also uses brain imaging. It examines the impact of retrieval orientation on how specific retrieval cues are processed (Rugg & Wilding, 2000). The critical comparison is of activity elicited by new (unstudied) items in the test phase under different retrieval goals (Fig 2B, comparison 2) As these items were not studied, this reflects the goals rather than retrieval itself (goal-related activity common to studied and new items can also be measured; Dobbins, Rice, Wagner, & Schacter, 2003). Given an established retrieval orientation, identical cues are processed differently according to what participants try to retrieve. In the example (Figure 2B), participants target words studied in either the deep or the shallow task. Alternative goals may relate to the format or location in which items were studied (see Mecklinger, 2010). Using this approach with ERPs, we found that older adults adopted a less distinctive retrieval orientation (Morcom & Rugg, 2004).

Converging evidence came from the third approach, the behavioral “memory for foils” paradigm (Jacoby, Shimizu, Velanova, & Rhodes, 2005). As in the second paradigm, analysis focuses on the new (unstudied) “foils” in the initial memory test (Figure 2B). A third task phase is now added to assess how these were processed under different retrieval goals (Figure 2C, comparison 3). It is thought that participants strategically boost recall in the initial retrieval phase by

internally reinstating the targeted (deep or shallow) study context in response to the word cues. This cue elaboration determines the level of processing applied to the foils: since “deep” foils are processed more meaningfully than “shallow” foils, memory is better for the deep foils in the final recognition test (Figure 2C). Unlike the first two (imaging) paradigms, which may detect any differential processing according to retrieval goal, this memory for foils effect depends on goal-specific reinstatement of the encoding context. Young, but not older, adults showed this effect.

A subsequent ERP study using the second paradigm examined age-related differences in retrieval orientation in a task requiring detailed recollection (Duverne, Motamedinia, & Rugg, 2009). In Morcom & Rugg’s (2004) and Jacoby et al.’s (2005) studies, initiation of recollection could be avoided if the simple “old” or “new” judgments were made on the basis of familiarity. Following Morcom & Rugg (2004), participants targeted items studied as either pictures or words, but in one condition recall of source information (screen location at study) was also required. This time, older adults successfully adopted a retrieval orientation, but only when source recall was required. This is consistent with the idea of a self-initiation deficit. But it also suggests that older adults can, under some circumstances, effectively initiate goal-directed retrieval. It is currently unknown whether, once engaged, this control is always as robust. A key factor may be whether retrieval goals compete, i.e., whether - unlike in Duverne et al.’s task - orientation to one type of to-be-retrieved information also requires rejection of items studied in other contexts or exclusion of other studied information. A recent fMRI study found that older adults’ prefrontal responses depended less than those of the young on which of two competing sources - study task or format - was

targeted. Prefrontal responses were also less tightly coupled with cortical regions carrying representations of the targeted information (Mitchell, Ankudowich, Durbin, Greene, & Johnson, 2013). This suggests impaired prefrontal goal maintenance, impeding ability to boost recall by reinstating study context in the posterior representation region. However, although the data implicate goal-directed control, they do not speak to whether this control acted before or after the point of retrieval.

The first three paradigms are critical for separating pre-retrieval control from retrieval itself, but it is also important to establish the “downstream” effects of control on what is recollected. The fourth approach assesses neural responses associated with successful retrieval, typically comparing responses to remembered studied items and correctly rejected unstudied items (“old/new” effects) (Figure 2B, comparison 4). Dywan et al. (1998) measured the degree to which the parietal ERP old/new effect, a neural correlate of recollection, favored targeted information (studied words) over non-targeted but familiar information (in this case, non-targets were novel words repeated during the test phase, but may also be studied items from a non-targeted context; Figure 2B). Target and non-target parietal effects were similar in magnitude in older adults, and in young adults performing a demanding secondary task during retrieval, suggesting recollection was less selective. Similar studies in adolescents and young adults have shown that the degree of recollection of to-be-excluded information tracks individual and developmental differences in cognitive control, and the speed with which retrieval orientation is engaged (Elward, Evans, & Wilding, 2013; Sprondel, Kipp, & Mecklinger, 2013)

Further examination of both pre-retrieval control and its downstream impact will be important because studies in young adults now point to more than one stage at which people can constrain what will be recollected (this work, like the studies of aging, has so far focused on goal-specific control; i.e., retrieval orientation rather than mode). Sometimes, it is possible to prevent recollection of non-targeted information entirely (“gating”; e.g., Morcom & Rugg, 2012). At other times, although there is irrelevant recollection this is constrained to some degree by the retrieval orientation (McDuff, Frankel, & Norman, 2009). This may indicate a second, later stage of constraint involving direct goal-dependent modulation of the neural reactivation during recollection (Elward & Rugg, 2015). A key question for aging research will be which of these stages is affected, and which preserved. Future studies should clarify how existing indices of pre-retrieval control relate to constraints on recollection, and it would be helpful to combine the different approaches. More definitive links are also needed between proactive control as measured in attentional paradigms such as the AX-CPT, and episodic pre-retrieval control. Elward & Wilding’s work in young adults has provided initial evidence that retrieval selectivity tracks individual and experimental variations in cognitive control.

Proactive control, reactive control and monitoring

The suggestion that aging impairs proactive control does not, of course, mean that this is its only effect on episodic memory. Control difficulties likely also impact encoding (e.g., Old & Naveh-Benjamin, 2008), and what occurs after information is retrieved. The source monitoring framework outlines reflective, self-generated processes required to specify the source, or context, of our mental experiences

(Johnson & Raye, 2000). Proactive cue elaboration processes are part of the framework, but a central focus is on monitoring the products of recall to prevent memory errors. Some of these reactive processes also depend on prefrontal cortex and are altered in aging (for review see Gallo, 2006). Behavioral data indicate that older adults are less likely to engage specific monitoring strategies, such as recall-to-reject (“I know I didn’t see this item, because I remember hearing it”) to avoid memory errors. Susceptibility to errors is also greater in individuals with poorer prefrontal function as measured using standardized cognitive tests.

One possibility is that proactive and reactive memory control both suffer as a result of prefrontal cortex decline. However, impaired proactive control may also increase demands on reactive control (Braver & West, 2008). At least in attentional tasks, reactive control may even be spared (Bugg, 2014). The “load-shift” hypothesis proposes that impaired recollection primarily reflects pre-retrieval difficulties, with a consequent greater shift to, and load on, post-retrieval monitoring (Velanova, Lustig, Jacoby, & Buckner, 2007). Consistent with this, older adults show *increased* neural activity during post-retrieval monitoring which is less goal-specific (McDonough, Wong, & Gallo, 2013). If this proposal is correct, alterations in post-retrieval monitoring and evaluation may reflect a form of compensation for proactive failure (for a similar view see (Dew et al., 2012)). The degree to which pre-retrieval and post-retrieval impairments co-exist or trade-off against one another is a key question for future research. It should also inform interpretation of findings of additional brain activity in older adults in imaging studies (Morcom & Johnson, 2015).

Conclusions

Current data support a *prima facie* case that initiation of episodic memory retrieval is impaired in aging, impairing ability to direct retrieval according to goals (see also Wilkens, Erickson, & Wheeler, 2012). But the details remain to be established. To borrow an expression from Light (1991), there are three main (non-exclusive) “hypotheses in search of data”. The first is that initiation of proactive control is impaired, but once initiated, the control is effective (Duverne et al., 2009; Morcom & Rugg, 2004). The second assumes that establishment of control is impaired only in the presence of interference, consistent with findings from studies of temporary memory and attention (Gazzaley, 2013). The third proposes that control can be established but is less effective in terms of “downstream” constraint of what is retrieved (Dywan et al., 1998).

These questions bear critically on how older adults should best respond to memory difficulties. In a recent review, Lindenberger and Mayr (2014) suggested that the environmental support account can explain a range of age-related differences in perceptual and attentional function as well as memory. Pinpointing the nature of memory difficulties is important not only for understanding them but also for training and remediation: should reliance on the kinds of inner control strategy optimal in youth be encouraged, and training aimed at bolstering these abilities, or are aging brains best advised to lean more heavily on external cueing and support? As lifespans increase, and technologies improve, these decisions will be critical.

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